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The Osteology and Relationships of the Pliocene ground squirrel, *Citellus dotti* Hibbard, from the Ogallala Formation of Beaver County, Oklahoma

by

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Contents

List of Illustrations

List of Tables

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The Osteology and Relationships of the Pliocene ground squirrel, *Citellus (Buiscitellus) dotti* Hibbard, from the Ogallala Formation of Beaver County, Oklahoma

by Margaret Skeels Stevens

Abstract—Enough material of the Pliocene ground squirrel, *Citellus dotti* Hibbard, from Beaver County, Oklahoma, is known to give some idea of the dental variation in this species. The generalized dentition is at the otospermophilid grade of development. Skeletal characters do not indicate a close relationship to any of the Recent subgenera of *Citellus*. The skull has a moderately short and very broad rostrum; limbs are of a specialized fossorial type. The species is placed in a new subgenus, *Buiscitellus*.

INTRODUCTION

Remains of ground squirrels are fairly common in Pliocene deposits, but the fossils are usually fragmentary and postcranial elements are rarely found associated with the skull and jaws. During the summer of 1961 Professor Claude W. Hibbard of the University of Michigan found the skull, lower jaws and other parts of a skeleton of a ground squirrel in the Ogallala Formation of northwestern Oklahoma. Results of a study of this specimen are presented in this paper. This specimen (UMMP 44323) is referred to *Citellus dotti* Hibbard (1954: 329). It adds to our knowledge of the upper dentition of this species and makes possible additional remarks about its relationship to other Pliocene and Recent ground squirrels.

Besides the new material of *C. dotti*, the following specimens have been examined in the course of this study:

Citellus shotwelli, holotype (University of Oregon Museum of Natural History, UOMNH F-3596).

Citellus wilsoni, holotype (UOMNH F-4097) and referred (University of California Museum of Paleontology, UCMP 55611).

Citellus gidleyi, holotype (UCMP 26793).

Citellus argonautus, holotype (UCMP 34281).

Citellus matachicensis, holotype, (Los Angeles County Museum, California Institute of Technology Collection, LACM, CIT 3551).

Citellus cocheisi, holotype (U.S. National Museum, USNM 10,490).

Citellus bensoni, holotype (USNM 10531).

Citellus dotti, holotype (University of Michigan Museum of Paleontology, UMMP 29769); paratypes (UMMP 29770, 30337), and referred specimens (UMMP 50641, 50643, 41128 and 30338).

Citellus howelli, referred specimens (UMMP).

Citellus rexroadensis, referred specimens (UMMP).

OCCURRENCE

Specimen nos. UMMP 29769, 29770, 30338, 41128, 50641, 50643, and 30337 were recovered from the uppermost part of the Ogallala Formation, upper Middle Pliocene (Late Hemphillian) (Tihen, 1955: 238), Buis Ranch local fauna locality, NE¼ SE¼ Sec. 5, T. 5 N., R. 26 E.C.M., Beaver County, Oklahoma. This site was discovered in 1951 and was visited by me during the summers of 1961 and 1962. During the field season of 1961 Dr. Claude Hibbard discovered the new ground squirrel skeleton (UMMP 44323) in an exposure approximately three-fourths mile east by north of the Buis Ranch local fauna locality, upper part of the Ogallala Formation, Buis Ranch, NW¼ Sec. 4, T. 5 N., R. 26 E.C.M., Beaver County, Oklahoma. The Ogallala Formation in this area is incompletely studied. For a discussion of the geology of the Buis Ranch local fauna locality see Hibbard (1954: 340–342). For discussions of the Ogallala Formation in general see Frye and Leonard (1957; 1959), Frye, Leonard, and Swineford (1956), and Cronin (1961).

This new locality was not visited by me until the summer of 1962. It is an exposure along a small intermittent stream and is composed of buff-colored silts and fine sands, with an incompletely indurated "mortar bed" toward the top. The exposure varies from 10 to 18 feet high and lies near the edge of a sink in which these sediments have been preserved. Parts of the Ogallala Formation have been preserved due to low topographic position of the deposits in various parts of this region as the result of collapse within the underlying Permian formations. This complicates the demonstration of continuity of the stratigraphy. A jaw of a large species of *Prosthennops* (UMMP 45691) and remains of *Nannippus minor* (Sellards) (UMMP 38409) and *Vulpes* sp. (UMMP 38426) have been found at the locality where the ground squirrel skeleton was found. A jaw of *Tanupolama vera* (Matthew) (UMMP 30203) was recovered approximately halfway between the Buis Ranch local fauna locality and the new site (Hibbard, 1963).

SYSTEMATIC DESCRIPTION

Order RODENTIA Bowdich, 1821

Family SCIURIDAE Gray, 1821

*Buiscitellus** subgen. nov.

Citellus dotti Hibbard, 1954

Figs. 1 and 2

Citellus dotti Hibbard, 1954: 329–352, Fig. 3.

The original description of this species is based on three rami. The holotype, UMMP 29769, consists of a right ramus bearing P_4-M_3. Paratypes, UMMP 29770 and 30337, consist of rami containing P_4-M_2 and M_1-M_3, respectively. A number of isolated teeth, UMMP 30338, 50641 and 50643 were

* *Buis*—refers to the Buis Ranch from which the fossil was recovered; *Citellus*.

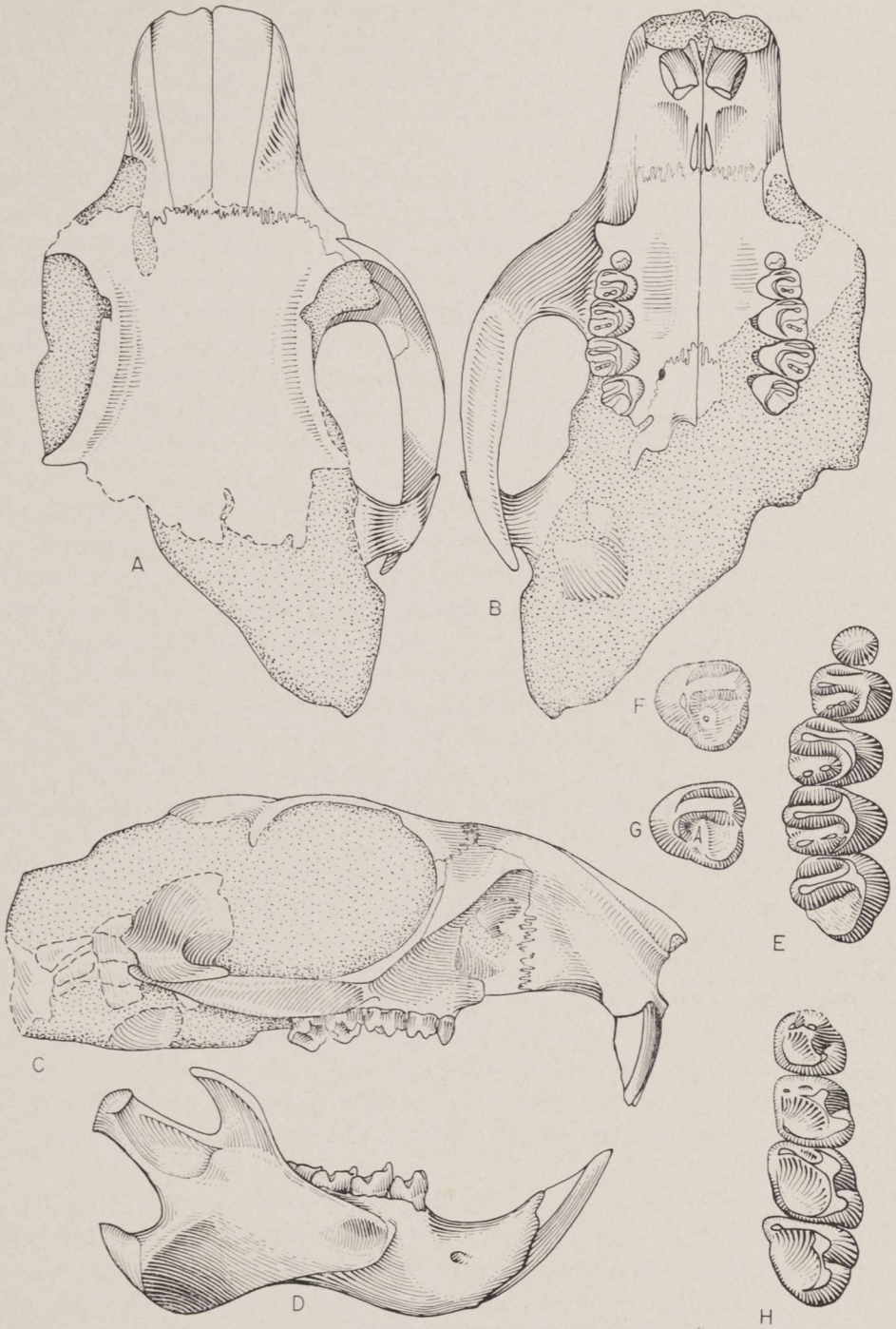

Fig. 1—Skeletal elements of *Citellus (Buiscitellus) dotti* (UMMP 44323). A-B, Dorsal view of skull, X 2; C-D, lateral view of skull and lower jaw, X 2; E, right toothrow, P^3–M^3, X 4; F, LM^3 (UMMP 50641), X 4; G, LM^3 (UMMP 50643), X 4; H, right toothrow, P_4–M_3, X 4.

also recovered and these were referred to the same species. On July 30, 1961, Claude W. Hibbard recovered a partial skull, both jaws, and part of the skeleton, UMMP 44323, of another individual of this species.

Type of the subgenus.—Citellus dotti Hibbard. The characters of the subgenus are those of the type species.

Amended diagnosis.—Citellus dotti is smaller than Recent *C. beecheyi beecheyi* (Richardson), possesses a relatively broader, parallel-sided rostrum, slightly less compressed cheek teeth and shorter, relatively stouter legs.

Hibbard (1954: 349) in the original description which was based on jaw fragments, states that *C. dotti* is "slightly larger than *Citellus fricki* Hibbard," another Hemphillian ground squirrel. *C. fricki* in turn is "slightly larger than *Citellus franklinii*," a living species (Hibbard, 1942: 253). The lengths of the upper and lower toothrows of *C. dotti* are in fact greater than those of *C. franklinii* (Sabine). The skull and skeleton, however, are considerably smaller than this Recent species.

Dentition.—For measurements of teeth see Tables 1 and 2. Both upper and lower incisors are stout and transversely compressed. The upper incisors are recurved and resemble those of Recent *Citellus annulatus* (Audubon and Bachman). The enamel, which is orange, originates on the anteromedial surface of the upper incisors and covers their anterior faces, ending approximately one third of the way posteriorly on the external surface. On the lower incisors the enamel begins on the anteromedial angle, covers the anterior faces, and ends approximately one-half of the way posteriorly on the external side. The coloration of the upper incisors is more intense than that of the lowers. The enamel is also crenulated to the slight degree observed in Recent *C. variegatus* (Erxleben).

Some bone is missing on the right side of the rostrum which permits observation of the incisor. The right incisor originates dorsomedial to the masseteric tubercle. The lower incisors originate slightly behind the M_3's and are much more procumbent than the uppers.

The teeth of both sides of the jaws agree in all morphological features except as noted. The P^3's (UMMP 44323 and 30338) are conical. They are approximately one-fourth the size of the P^4's and their crowns are moderately high. The P^3, UMMP 44323, is slightly simpler than 30338, but this may be a result of poor preservation. The P^3 (30338) possesses a slight posterior cingulum.

The P^4 is a little smaller than M^1. The cheek teeth are little compressed and none interlocks with its neighbor (Fig. 1, E). The protoloph on M^1-M^3 is well developed. The metaloph on P^4-M^2 is as high as the protoloph, and is separated from the respective protocones. This separation decreases progressively from P^4-M^2. On M^2 the metaconule is connected to the base of the protocone by a low, narrow ridge of enamel. The metaconules on P^2-M^2 are oval. The metaloph also increases in length from P^4-M^2. On P^4 the metacone and metaconule are separated only by a slight sulcus. The distance between

TABLE 1

Measurements* of upper teeth of *Citellus dotti*

Anteroposterior diameter Specimen number	I	P^3	P^4	M^1	M^2	M^3
44323	3.23	1.30	2.33	2.34	2.50	2.70
.....	3.23	.....	.....	2.34	2.52	2.78
30338	.....	1.35	.....	2.4	2.7	3.3
.....	.....	.....	.....	.....	2.8	3.4
.....	.....	.....	.....	.....	2.9	3.2
.....	.....	.....	.....	.....	2.7	.....
.....	.....	.....	.....	.....	2.8	.....
.....	.....	.....	.....	.....	2.8	.....
.....	.....	.....	.....	.....	2.8	.....
.....	.....	.....	.....	.....	2.5	.....
.....	.....	.....	.....	.....	2.6	.....
.....	.....	.....	.....	.....	2.7	.....
50641	.....	.....	.....	.....	.....	3.1
50643	.....	.....	.....	.....	.....	3.2
Transverse diameter Specimen number						
44323	1.75	1.46	2.91	3.13	3.34	3.07
.....	1.82	.....	2.91	3.12	3.37	3.10
30338	.....	1.3	.....	2.8	3.6	3.3
.....	.....	.....	.....	.....	3.7	3.0
.....	.....	.....	.....	.....	3.4	3.3
.....	.....	.....	.....	.....	3.5	.....
.....	.....	.....	.....	.....	3.5	.....
.....	.....	.....	.....	.....	3.5	.....
.....	.....	.....	.....	.....	3.1	.....
.....	.....	.....	.....	.....	3.2	.....
.....	.....	.....	.....	.....	3.2	.....
.....	.....	.....	.....	.....	3.5	.....
50641	.....	.....	.....	.....	.....	3.3
50643	.....	.....	.....	.....	.....	3.4

* Measurements in this and other tables are in millimeters. Both right and left sides are included.

the metacone and metaconule on P^4-M^2 increases as the length of the metaloph increases. On P^4-M^2 the protoloph and metaloph are not markedly convergent toward the protocones. Small mesostyles are present on M^1-M^3 (barely indicated on LM^1). Anterior cingula are present on all molariform teeth and blend with the respective protocones without an abrupt change of direction. On P^4 the anterior cingulum occurs as a small ridge well down the anterior face of the tooth. The cingulum becomes more prominent on the

molars and is largest on M^2. The anterior cingulum is not connected to the protocones on P^4-M^1. It is connected on M^2-M^3 as in Recent *C. beecheyi*, *C. variegatus*, and *C. annulatus*. Parastyles are present. All M^3's are wider than long. Those of UMMP 44323 have simple basins, though the RM^3 has a slight "metaconid" swelling on the floor of the basin. Of the five isolated M^3's, two (UMMP 50641 and 50643) have basins in which small metaconules occur. On M^3 (50641) this conule is conical (Fig. 1, F) whereas on M^3 (50643) it is elongated anteroposteriorly (Fig. 1, G). These two teeth are clearly those of *C. dotti* and agree with the other M^3's known for that species in all other respects. Apparently, the M^3's of the *C. dotti* population were variable. Such variability also occurs among M^3's of Recent *C. beecheyi*.

All known teeth of *C. dotti* were examined. The form of the lower series of the supplemental material (Fig. 1, H) agrees with the original description (Hibbard, 1954: 350). In all specimens P_4 is rounded anteriorly. The protoconid and parametaconid on P_4 are not particularly appressed and are separated from each other by a moderately deep sulcus. The protoconid and parametaconid on P_4 of Recent *C. beecheyi* are usually close together. The presence of protoconulids (anterior cingula or paraconulids of some authors) cannot be confirmed on the new specimen as both P_4's are damaged. A protoconulid occurs on the holotype, UMMP 29769, and specimen 41128. M_1 and M_2 are rhombohedral, and are a little, though variably compressed anteroposteriorly. Posteriorly closed trigonid basins are present on M_1-M_2 but are not found on M_3. The trigonid is little elevated above the talonid on any of the molars. On M_1-M_3 the parametaconids are much higher than the protoconids and the protoconids are slightly higher than the hypoconids in the manner observed in the Recent subgenus *Otospermophilis*. The ectolophids are moderately well developed and as external in position as in Recent otospermophilids. The hypoflexids (Stirton and Goeriz, 1942: 464) are U-shaped and moderately deep. These are perpendicular to the ectolophids and not oblique as in some species of ground squirrels. Posterolophids are also well developed. There are small endoconids on P_4-M_2, however, and they are very small on P_2. Notches occur anterior to the endoconids, and small mesostylids lie in front of these. The mesostylids are expressed as slight swellings on the ridge as it resumes and swings upward to meet the base of the metaconid. There are no mesoconids. The depth of the talonid basins is variable. This tends to increase the apparent prominence of the ectolophids in some specimens. The basins are not broad.

Skull.—The skull, UMMP 44323 (Fig. 1, A-C), lacks the cranium and left zygomatic arch. The rostrum is moderately short, very wide above the incisors, and nearly parallel-sided. The width of the rostrum, as measured across the premaxillaries at their maximum diameter just behind the external naries, is approximately the same as that between the apices of the P^3's. Very little vertical compression of the rostrum has occurred. This type of rostrum does not occur among living *Citellus*, but is not unlike that of *Marmota*. The nasals

TABLE 2

Measurements of lower teeth of *Citellus dotti*

Anteroposterior diameter Specimen number	I	P_4	M_1	M_2	M_3
44323	3.00	2.17	2.32	2.54	3.04
----------	------	------	------	2.57	2.97
29769	------	2.20	2.46	2.61	3.01
29770	------	2.3	2.5	2.9	------
41128	------	2.2	2.5	2.8	------
30337	------	------	2.4	2.8	3.2
30338	------	------	------	------	3.2
Transverse diameter Specimen number	I	P_4	M_1	M_2	M_3
44323	1.59	2.46	2.62	2.96	3.03
----------	1.59	------	------	2.96	3.04
29769	------	2.51	3.11	3.25	3.16
29770	------	2.3	2.7	2.95	------
41128	------	2.4	3.1	3.4	------
30337	------	------	2.8	3.3	3.1
30338	------	------	------	------	3.5

are short and broad and do not extend posterior to the premaxillary-frontal suture. The supraorbital and postorbital diameter of the skull are relatively great; they resemble the proportions in the subgenus *Notocitellus* Howell. The supraorbital foramina are open externally but the opening is constricted. The postorbital processes are similar to those of Recent *Citellus beecheyi*. The zygomatic plate is fully developed and steep. Masseteric tubercles are large and the incorporated infraorbital foramina are triangular with dorsal apices. Depressions for the cheek-pouch musculature are well developed and much more rectangular anteriorly than in Recent *C. beecheyi* or *C. variegatus*. The diastema of the skull is relatively shorter than in these Recent species. The preserved zygomatic arch is moderately strong but does not appear to have expanded greatly posteriorly; as a result the skull seems rather parallel-sided and thus resembles that of Recent *C. (Notocitellus) annulatus*. The zygomatic arch is more expanded anteriorly than in Recent *C. beecheyi* or *C. annulatus*. The ventrolateral margin of the arch is inflected to the degree observed in Recent *Citellus* and no suborbital process is present. The posterior border of the zygomatic plate of the maxillary is opposite the middle of M^1 as in all ground squirrels. The toothrows do not markedly converge posteriorly and are almost parallel to the basicranial axis. The exact location of the palatal foramina is uncertain owing to the poor preservation of the posterior region of the skull. They appear to lie posterior to the anterior extension of the palatine-maxillary suture.

Lower jaw.—The lower jaws (Fig. 1, D) resemble those of Recent *C. beecheyi* and *C. annulatus* in general conformation. The mandibular and subcondylar notches are relatively deeper and narrower than those of the subgenera *Otospermophilus* and *Notocitellus*. The coronoid and angular processes are relatively close together. The condyles are longer anteroposteriorly than transversely. The maximum ventral emargination of the jaw occurs posteriorly, under M_3. (In Recent *C. beecheyi* and *C. variegatus* it occurs generally under M_2.) The diastemal depression of the jaw is shallow, as in the subgenera *Otospermophilus* and *Notocitellus*. The diastema of the lower jaw of *C. dotti* does not appear proportionally shorter than in some specimens of Recent *C. beecheyi*, whereas in others it is distinctly shorter. The inflection of the ventral margin of the angular process is pronounced as in most Recent ground squirrels. The scar for *M. masseter lateralis profundus, pars anterior* ends under the forward edge of M_1 and the scar for *M. masseter medialis, pars anterior* ends slightly anterodorsally, under the hypoconid of P_4. These scars are not pronounced.

The postcranial skeleton recovered consists of three cervical, two dorsal, three lumbar vertebrae, the sacrum, and one caudal vertebra, glenoid of the left scapula, both humeri lacking proximal epiphyses, the radii and ulnae, right tibia, the epiphyses of the left tibia, right calcaneum and various toe bones. For measurements of these elements see Table 3.

Vertebrae.—The cervical vertebrae are represented by the third, fourth, and fifth. These are almost complete. Two dorsal vertebrae are known, probably the third, and the eighth. The neural spines are gone but the remaining parts are only slightly smaller than those of small adults of Recent *C. beecheyi*. The lumbar vertebrae are the fifth, sixth, and seventh. They lack parts of the transverse processes and neural spines. One completely preserved eight-caudal vertebra was also recovered. It is only slightly smaller than the corresponding vertebra in small individuals of Recent *C. beecheyi*.

Sacrum.—The sacrum is composed of four fused vertebrae (Fig. 1, H). The number of fused sacral vertebrae varies from three to four among living ground squirrels, even within the same species (Bryant, 1945: 291). *C. dotti* (UMMP 44323) is the second Hemphillian ground squirrel known to possess the advanced number of four vertebrae in the sacral complex (see Wilson, 1949: 172).

Pelvis.—Both halves of the pelvis lack the ischium (Fig. 2, G). The iliac wings are similar to those of other ground squirrels and thus unlike those of *Cynomys* or *Marmota*. The pelvis resembles that of Recent *C. beecheyi* closely but possesses a considerably larger acetabulum relative to the size of the pelvis.

Humerus.—The deltoid crest on the humerus (Fig. 2, A-C) of *C. dotti* is more prominent and extends farther down the shaft than in 21 skeletons of Recent *C. beecheyi* examined. The crest is also larger than in numerous skeletons of other species of ground squirrels compared. This implies a large

TABLE 3

Measurements of skeletal elements of *Citellus dotti* (UMMP 44323)

Length of toothrow, P^3-M^3	10.84
Length of diastema, I-P^3	11.41
Breadth between apices of P^3's	10.70
Breadth of rostrum above incisors	9.95
Interorbital diameter at notches	12.60
Postorbital constriction	15.30
Length of toothrow, P_4-M_3	10.16, 10.48
Length of diastema, I-P_4	7.78
Length of lower jaw, posterior margin of condyle to anterior tip of symphysis	34.0, 33.4
Depth of jaw below M_1	8.0, 8.1
Length of right humerus, epiphyseal surface to distal end	33.8
Length of ulna, proximal margin of olecranon process to distal epiphyseal surface	35.1, 35.0
Length of radius, proximal articular surface to distal epiphyseal surface	27.9, 27.9
Length of left femur	42.9
Length of right femur, proximal end to distal epiphyseal surface	39.9
Length of right tibia	44.0
Length of pelvis, proximal ilium margin to distal ischial margin	39.5, 39.1
Length of sacral complex, anterior to posterior margins of centra	20.9
Length of right calcaneum	9.7
Width of right calcaneum	6.1

M. deltoideus which abducts the foreleg. The lateral epicondylar crest is slightly eroded on the right humerus but its proximal end is completely preserved on the other. It is greatly expanded laterally. The crest extends up the shaft to a point almost opposite the distal termination of the deltoid crest. The lateral epicondylar crest on humeri of Recent species do not extend as far up the shaft. Entepicondylar foramina are present. The humeri are slightly more robust with broader articular surfaces and larger muscular attachments than in Recent *Citellus*.

Ulna.—The forward edge of the ulna is straight. The olecranon process is slightly larger relative to the size of the ulna than in Recent *C. beecheyi* and the semilunar notch is also larger. This slight enlargement of the olecranon process may indicate a well-developed triceps muscle complex which extends the forelegs.

Radius.—The radius differs from those of any Recent ground squirrel

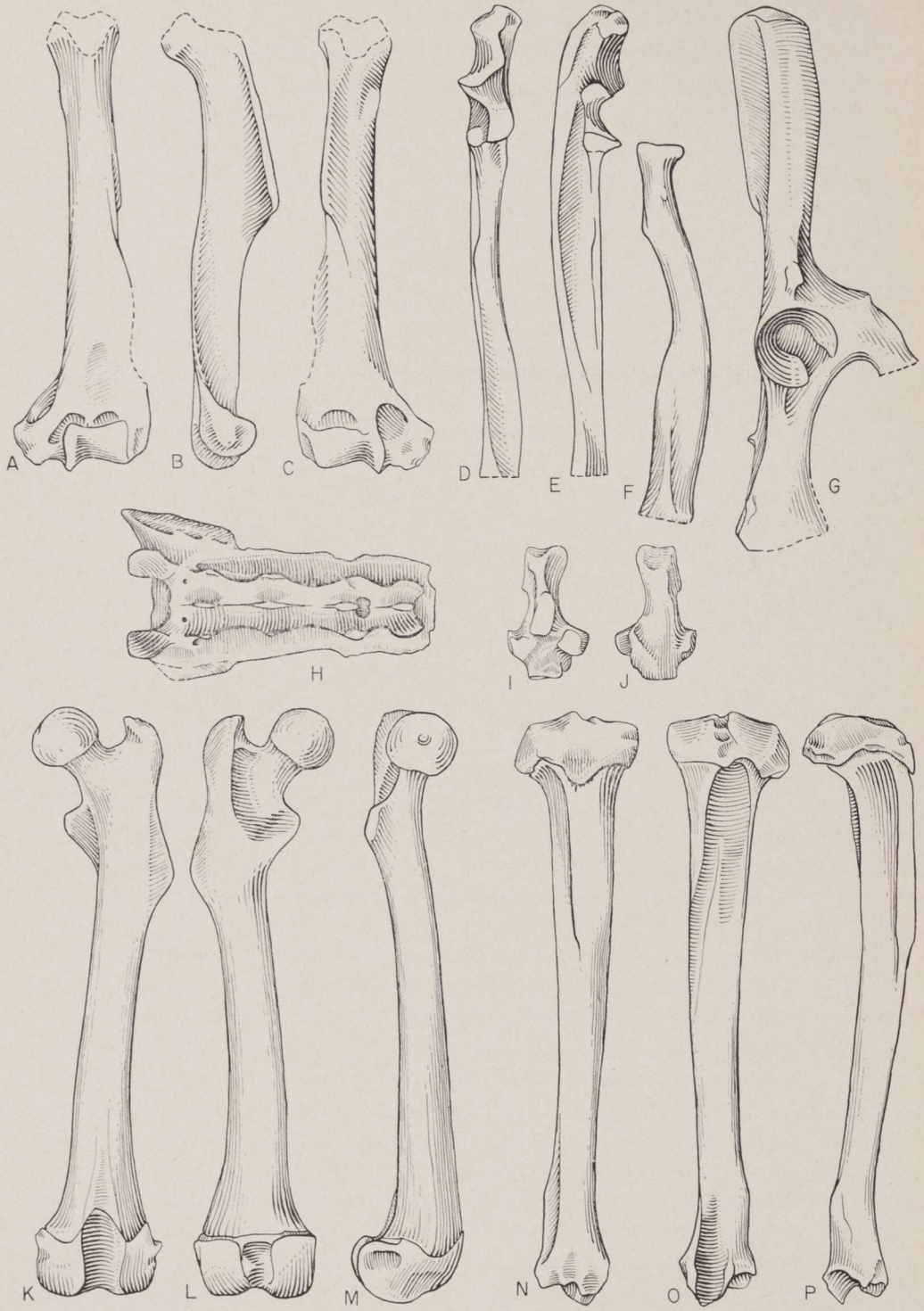

Fig. 2—Postcranial elements of *Citellus (Buiscitellus) dotti* (UMMP 44323). A-C, posterior, external and anterior view of right humerus; D-E, anterior and external view of right ulna; F, external view of right radius; G, external view of right pelvis; H, dorsal view of sacral complex; I-J, dorsal and ventral view of right calcaneum; K-M, anterior, posterior and external view of left femur; N-P, anterior, posterior and external view of right tibia. All X 2.

examined. It is short, very bowed and transversely broad along the distal portion. In this portion it is also markedly compressed on the anteroexternal and posterointernal surfaces. The radius is as bowed as in *Marmota*, but much more compressed distally. It also resembles the radius of some individuals of *Cynomys*. When the ulna and radius are articulated a large space results between the straight anterior margin of the ulna and the concave posterior edge of the radius. This space is much larger than in specimens of Recent *Citellus* examined. Both the ulna and radius of *Cynomys* and *Marmota* are bowed, therefore such a space does not occur. The front leg of *C. dotti* is considerably heavier than that of living ground squirrels. The ulna of *C. dotti* would be only slightly longer than the humerus if the proximal epiphysis of the humerus and distal epiphysis of the ulna were present. The ulna is slightly shorter relative to the humeral length than in Recent *C. beecheyi*.

Femur.—The femur is similar to those of Recent *C. beecheyi*, but the articular surfaces are larger. The lesser trochanter extends posteromedially as in *Citellus*. It is long and pointed, and not conical as in *Cynomys* or *Marmota*. The third trochanter is situated slightly distal to the lesser trochanter as in ground squirrels and not opposite the lesser trochanter as in *Cynomys* or *Marmota*.

Tibia.—The curvature of the tibia is less than that in Recent *Citellus*, *Cynomys*, and *Marmota*, but more than in tree squirrels. The medial crest is prominent but no more so than in large individuals of Recent *C. beecheyi*. This ridge forms the insertion for a number of extensor muscles of the leg, among them *M. gracilis, pars anterior* and *M. semitendinousus*. These muscles are more powerful in fossorial than in non-fossorial squirrels. The popliteal fossa is deeper than that found in some Recent *C. beecheyi* and the lateral and medial crests are thus prominent. The medial crest is the more prominent of the two. The popliteal line is well defined and forms the boundary for the origin of *M. flexor digitorum longus*. This attachment is more prominent in the fossil than is usual in the tibia of Recent *C. beecheyi* and other ground squirrels. Distally the process for the union of the tibia with the fibula and the medial malleolus is short as in ground squirrels. The tibia and femur in *C. dotti* are about the same length. They resemble those of Recent *C. beecheyi* much more closely than do the humerus and radius.

Calcaneum.—The right calcaneum (Fig. 2, I-J), though only slightly smaller than those of Recent *C. beecheyi* has a proportionally shorter proximal (tuber) process.

The skeleton of *C. dotti* is that of a moderately small, heavy-bodied ground squirrel with short limbs, the distal segments of which are almost the same length as the proximal. The articular surfaces on the limb bones are large. Muscle attachments are large.

Citellus mckayensis Shotwell (Shotwell, 1956: 728) of the Hemphillian of Oregon will not be discussed in detail as it is considerably advanced over the otospermophilid dental grade of evolution and thus bears no immediate relationship to *C. dotti*.

The P^3's in *C. dotti* (UMMP 44323 and 30338), *C. matachicensis*, *C. wilsoni* (Wilson, 1949: 171) (LACM CIT 3551), and *C. fricki* Hibbard (Frick Collection; American Museum of Natural History, F:AM 24627) (Hibbard, 1942: 253) are simpler than in *C. shotwelli* (UOMNH F-3596) (Black, 1963: 202). All these P^3's are small, approximately one-fourth or less the size of the respective P^4's. Those of *C. fricki* are especially small. The P^3 of *C. wilsoni* (UCMP 55611) is approximately one-fourth as large as the P^4. Disregarding differences in gross size between these species, the relative sizes of the P^4's of *C. shotwelli* and *C. wilsoni* are somewhat less in relation to the M^1's than in *C. dotti* and *C. matachicensis*. The P^4-M^2 of *C. shotwelli* are set much closer together than in *C. dotti*, *C. matachicensis*, *C. wilsoni* or *C. fricki*, therefore they interlock with their neighbors. The metacones and metaconules of the P^4's of *C. dotti* are closer together than in *C. matachicensis* and *C. wilsoni*. These cones, however, are farther apart on the M^1's and M^2's of *C. dotti*, and the resulting metaloph is therefore longer than it is in *C. matachicensis*. The metacones and metaconules of *C. wilsoni* are farther apart on M^1 and M^2 than in *C. dotti*. The teeth of *C. shotwelli* and *C. fricki* are worn but apparently the metalophs were relatively long on P^4-M^2. Wilson (1949: 172) reports a "small but nearly obliterated metaconule is present in M^3" of *C. matachicensis*. The RM^3 of *C. dotti* (UMMP 44323) is similar. The metaconules in M^3's of *C. dotti* are variable, ranging from almost absent to small irregular complications in the basins of these teeth. Similar variability occurs among M^3's of Recent *C. beecheyi*. The worn M^3 of *C. shotwelli* must have had a slight swelling in this area, but no conule. The M^3's of *C. wilsoni* have very slightly uneven basins. The protocone of the M^3 in UCMP 55611 is also narrower than that of *C. dotti*. Furthermore, the protocone is set much closer to the protocone of M^2 than in the Buis Ranch specimen. The M^3 of *C. shotwelli* is more expanded posteriorly than that of *C. dotti*, *C. fricki*, or *C. matachicensis*.

Relative crown height is difficult to compare because of differences in tooth size between the various species and differences of occlusal wear between individuals. The crown height of *C. matachicensis*, however, appears greater than that of the other species. The upper and lower teeth of *C. shotwelli* resemble those of Recent *C. beecheyi* (Black, 1963: 204) more closely than the teeth of other species.

The hypoconid portion of the P_4's of *Citellus shotwelli*, *C. fricki*, *C. wilsoni* (UOMNH F-4097) (Shotwell, 1956: 728) and *C. matachicensis* is more expanded laterally than in the *C. dotti* material. This portion of the P^4's of

C. argonautus (Stirton and Goeriz, 1942: 462) and *C. gidleyi* (Merriam, Stock and Moody, 1925: 68) is similar to *C. dotti*. This apparent expansion is in part the result of appression of protoconid and metaconid which has narrowed the anterior portion of the tooth. These cones on the P_4 of *C. wilsoni* are not appressed, but the anterior portion of the tooth is nevertheless narrower than in *C. dotti*. Furthermore, the posterior margin of the P_4's of *C. shotwell*, *C. matachicensis*, and *C. wilsoni* are more obliquely inclined toward the axis of the toothrow than in the other species. This may, however, be a function of individual age. Trigonid basins are present on the teeth of all these species, except *C. fricki* where they have been lost by wear. They are deep and closed posteriorly on M_1-M_3 of *C. gidleyi*. Trigonid basins are also well developed on M_1-M_3 of *C. wilsoni*, but are open posteriorly. These basins are moderately well developed and closed posteriorly on the M_1's and M_2's only of *C. dotti*. Trigonid basins are shallow on M_1-M_3 of *C. shotwelli* and *C. matachicensis*, but they are open posteriorly on the last tooth. A trigonid basin is also present on the fragment of M_1 of *C. argonautus*. It is closed posteriorly. The depth of the trigonid basin varies among individuals of the same species of Recent ground squirrels, but the basin occurs consistently on the same tooth throughout the species.

The trigonid in these Hemphillian species is only moderately elevated above the talonid. That of *Citellus mckayensis* (referred to the subgenus *Citellus* by Shotwell, 1956: 229–230) is much higher.

Very little anteroposterior compression is observed in M_1 and M_2 of *Citellus wilsoni*. More is seen in *C. matachicensis* and *C. dotti* (UMMP 44323). Still more compression is present in the holotype of *C. dotti* (UMMP 29769), *C. shotwelli*, and *C. gidleyi*. The M_2 of *C. fricki* is especially compressed, internally. All M_3's of *C. dotti* are wider than long. The M_3's of the remaining species (except *C. fricki* where this tooth is lost), are slightly more expanded posteriorly, thus reducing the relative width of the tooth. Ectolophids are high in *C. wilsoni*, moderate in *C. gidleyi* and less prominent in *C. matachicensis*, *C. shotwelli*, *C. fricki*, *C. argonautus*, and *C. dotti*. The greater wear on the teeth of the last four species may account for this apparent reduction in the height of the ectolophids. The talonid basins are moderately deep in *C. dotti* and *C. gidleyi*. They are also moderately deep in *C. wilsoni*, but they are much broader than in the two previous species. Talonid basins are shallow in *C. shotwelli*, *C. matachicensis*, *C. fricki*, and *C. argonautus*, but again this may be a function of tooth wear in some of these species.

The skulls of *Citellus dotti*, *C. matachicensis*, and *C. wilsoni* (UCMP 55611) are not markedly different in gross size but considerable difference occurs in the relative proportions of the various parts. Ratio diagrams (Simpson, 1941) were constructed to compare graphically the relative proportions of these skulls. The rostrum in *C. dotti* is considerably broader anteriorly than in the other two species (Fig. 3, A and B). The rostrum in *C. wilsoni* is longer, that in *C. matachicensis* slightly shorter, than in *C. dotti*. The con-

figuration of the rostrum of *C. wilsoni* resembles rather closely the rostra of the subgenus *Otospermophilus, Notocitellus,* and *Callospermophilus.* (Fig. 4, B). The rostrum of *C. matachicensis* does not resemble that of any Recent ground squirrel studied. The rostra are nearly parallel-sided in *C. matachicensis* and *C. dotti,* and more tapering in *C. wilsoni.* The rostrum of *C. fricki* is long and slender (see Hibbard, 1942, Pl. 1. Figs. 1 and 5). The relative proportions of the interorbital breadth and postorbital breadth of *C. dotti* and *C. matachicensis* are similar. The postorbital breadth of *C. wilsoni* is more constricted. The orbits of *C. wilsoni* are notably smaller than those of *C. dotti* and *C. matachicensis.* The pits for the cheek pouch musculature are wider anteriorly in *C. dotti* than in *C. wilsoni, C. matachicensis,* or *C. fricki.* The zygomatic arches are convergent anteriorly in *C. matachicensis* but not in *C. dotti.* The zygomatic plate is similar in these two species. Masseteric tubercles are well developed in *C. matachicensis, C. wilsoni, C. dotti,* and *C. fricki.* The infraorbital foramina are triangular in the first three species, and slit-like in the last (Black, 1963: 212).

The supraorbital foramina are open in *C. matachicensis, C. wilsoni,* and *C. dotti.* The foramina in the specimen of *C. fricki* have broken margins so it

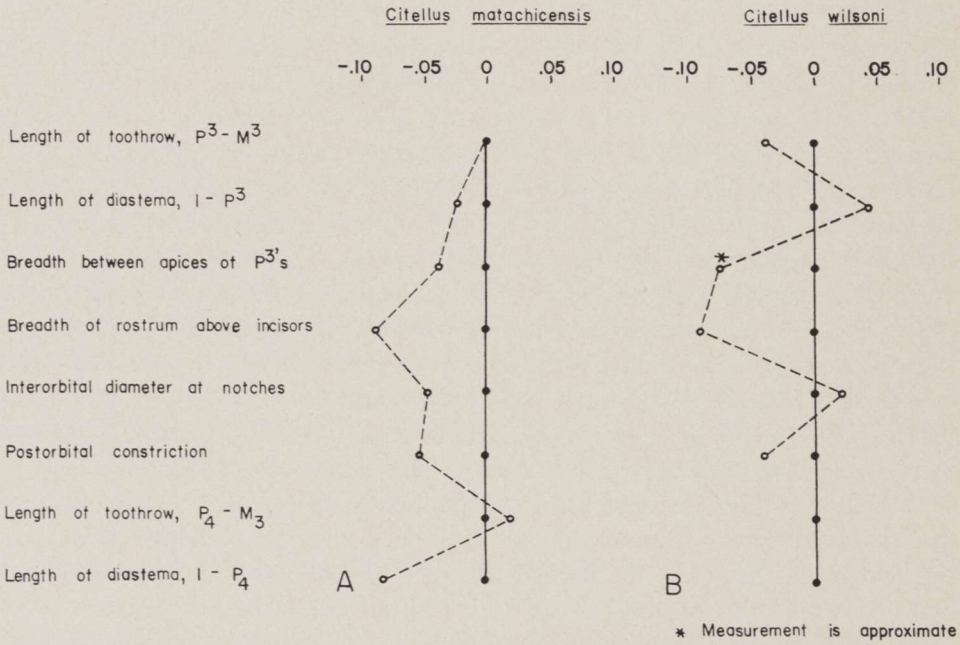

Fig. 3—Ratio diagrams, after Simpson (1941), comparing measurements of corresponding regions of the skull and jaws of various Pliocene ground squirrels. Solid line in both diagrams represents the standard, *Citellus (Buiscitellus) dotti* (UMMP 44323) of the uppermost Hemphillian. Dashed line, A, represents *C. matachicensis* (LACM CIT 3551) of the Hemphillian; dashed line, B, represents *C. wilsoni* (UCMP 55611) of the Clarendonian. The horizontal scale represents the deviation from the standard of the logarithm of each dimension. No vertical scale is used. *C. (Buiscitellus) dotti* shows different cranial and mandibular proportions than the two other species. The proportions seen in *C. wilsoni* are not unlike those seen in Recent *C. (Otospermophilus).*

is not known whether they were closed (Hibbard, 1942: 254). The supraorbital and postorbital width (interorbital diameter at notches, and postorbital constriction) of *C. dotti* is greater than *C. matachicensis*, and less than in *C. fricki* and *C. wilsoni*. The supraorbital width of the skull of *C. fricki* is slightly greater than the postorbital width. The opposite is true for the three other species.

Of the species discussed, five are represented by fairly complete lower jaws. The jaw of *Citellus shotwelli* resembles that of *C. dotti*, but neither of these resembles the jaw of *C. matachicensis*. The diastema of the latter is very short, that of *C. dotti* and *C. fricki* medium, and that of *C. shotwelli*, longer. The great size of the lower incisor and the mandibular notch of *C. fricki* are similar to those of *Sciurus*. The diastemal depression of *C. matachicensis* is very shallow, that of *C. argonautus*, *C. shotwelli*, *C. gidleyi*, *C. dotti*, *C. fricki*, and *C. wilsoni* are slightly more excavated. The ventral emargination of the jaw occurs under M_1 in *C. matachicensis*, and under M_2 in *C. gidleyi* and *C. shotwelli*, between M_2 and M_3 in *C. wilsoni* and *C. fricki*, and under M_3 in *C. dotti*. *C. matachicensis* also has a relatively broader condylar and coronoid process than *C. shotwelli* and *C. dotti*, and probably *C. wilsoni*. The specimen of *C. wilsoni* is broken in these areas but otherwise the jaw agrees rather well with that of *C. shotwelli* and Recent *C. variegatus*. The condyles of *C. dotti* and *C. fricki* are broader anteroposteriorly than transversely. Those of *C. shotwelli* and *C. matachicensis* are broader transversely.

Some postcranial skeletal parts of *C. shotwell*, *C. matachicensis*, and *C. fricki* are known and the elements shared with those of *C. dotti* will be discussed. The humerus of *Citellus matachicensis* is represented by proximal epiphyses only; that of *C. fricki* is complete. The humerus of the latter species resembles that of *C. variegatus* but is slightly smaller (Black, 1963: 213). The ulna of *C. matachicensis* is very slightly larger and that of *C. shotwelli* is much larger than that of *C. dotti*. The ulna of *C. shotwelli* is as long as large specimens of Recent *C. variegatus* but slightly more slender. The radius of *C. matachicensis* is slightly longer than that of *C. dotti* but not appreciably heavier. The radius of *C. dotti* is more bowed, and slightly more compressed distally. The radius in *C. shotwelli* is again much longer and not as bowed or compressed as in *C. dotti*. The ulna and radius of *C. fricki* are somewhat smaller than those of *C. variegatus* but the ulna possesses a shallow lateral fossa (Black, 1963: 213). The ulna and radius of these two species are considerably larger than the corresponding bones of *C. dotti*.

The femur of *Citellus matachicensis*, represented by a proximal end, is nearly the same size as that of *C. dotti*, but the head is considerably smaller. The tibia of *C. matachicensis* is represented by a fragment of the distal end and is smaller than in *C. dotti*. The distal articular surfaces of tibiae of *C. shotwelli* and *C. dotti* are the same size. It will be recalled that the front leg of *C. shotwelli* was much larger than that of *C. dotti* and close to large indi-

viduals of *C. variegatus* in size. *C. matachicensis* and *C. shotwelli* thus tend to have slender hind legs; those of *C. dotti* are heavier.

The sacrum is known for *Citellus matachicensis* and *C. dotti*. The specimen of *C. matachicensis* has not been completely removed from matrix but it appears to be only slightly larger than that of *C. dotti*. Both sacra are composed of four fused vertebrae. This fusion occurred before the young adult stage. The pelves of both species are very nearly the same size, but the acetabulum of *C. dotti* is the larger.

Occurring with *Citellus dotti* in the Buis Ranch local fauna is a larger ground squirrel referred to *C. rexroadensis* Hibbard. The species was originally described from an Upper Pliocene deposit in southwestern Kansas (Hibbard, 1941: 348). If the identification of the *C. rexroadensis* material from the Buis Ranch local fauna is correct this species has a range from late Middle to late Upper Pliocene time (Hazard, 1961). The lower teeth (UMMP 34738) of *C. rexroadensis* from the Buis Ranch local fauna locality are less complicated than those known from younger localities. This specimen differs from *C. dotti* in larger size, more anteroposterior compression of M_1 and M_2, and longer and more triangular M_3. In addition, the parametaconid of the M_3 extends much farther anterointernally, and therefore lies much closer to the entoconid of the M_2 than in *C. dotti*. Hypoflexids in *C. rexroadensis* are posteriorly curving, V-shaped notches. The diastemal depression is greater, the rostrum juts more horizontally forward, and the maximum ventral emargination of the lower jaw occurs under M_2 in *C. rexroadensis*. Specimens of *C. rexroadensis* from the Upper Pliocene show a tendency toward slightly greater size, deeper diastemal depressions, further increase in size of M_3 and indications of a shallow basin trench on M_1-M_3, as this term is used by Repenning (1962, Fig. 2). The dentition of *C. rexroadensis* is considerably advanced over that of *C. dotti*. The P^3 is larger, possesses an anterior and posterior cingulum and a transverse cutting apex; M^1 and M^2 are more compressed, and M^3 has the beginnings of a metaloph.

All the species discussed, with the exception of *Citellus mckayensis* and possibly *C. rexroadensis*, represent ground squirrels at the otospermophilid grade of dental evolution. Other than that, they represent very different animals with undoubtedly different ways of life. *C. shotwelli*, *C. matachicensis*, and *C. fricki* can be more satisfactorily compared with *C. dotti* because in addition to their dentitions, parts of their postcranial skeletons are known. *C. shotwelli* represents a species with large front legs and slender hind legs; these proportions in *C. fricki* were essentially like those of Recent *C. variegatus*. *C. matachicensis* possesses slightly longer but more slender limbs than *C. dotti*, but was probably fossorial also. *C. fricki* and *C. shotwelli* were probably scampering, terrestrial squirrels which were, to some extent, fossorial. *C. dotti* may have been more fossorial than most of its contemporaries.

From the Pliocene otospermophilid radiation came the progenitors of living *Otospermophilus*. This radiation undoubtedly produced numerous phy-

letic lines of terrestrial and (or) fossorial squirrels, adapted to Pliocene environments that were later to be replaced by more advanced, aggressive citellids when these environments changed. The advanced modern speciation for the most part was probably contemporary with the development of intermittent Pleistocene aridity.

Bryant (1945: 365–367) and Wilson (1960: 64–65) have suggested generalized characters which they recognized in Oligocene and Lower Miocene sciurids. More material, including fossil specimens, was available to Wilson and his suggestions are slightly different from Bryant's. The two agree, however, on the following: (1) braincase low; (2) rostrum massive and broad anteriorly; (3) mandible with short diastema and shallow diastemal depression; (4) masseteric fossa deeply concave, ending under M_1; (5) incisors stout; (6) P^3 small; (7) P^4 smaller than M^1; (8) upper cheek teeth with wide protocones, convergent metalophs and protolophs toward protocones, and metalophs not connected to the protocones; (9) metaconules and mesostyles present; (10) M^3 longer than wide; (11) P_4 with appressed protoconid and metaconid; (12) M_3 elongated; (13) low trigonids; and (14) mesoconids and mesostylids present.

Thus, *Citellus dotti* combines generalized and specialized characters. It is shown to be a ground squirrel by: (1) position of zygomatic notch; (2) inflection of ventral border of zygoma; (3) type of infraorbital canal; (4) no suborbital process of jugal; (5) pits for the cheek-pouch muscles strongly developed; (6) development of P^3; (7) enlargment of P^4; (8) and position of masseteric fossa on mandible. As noted, its teeth are at the otospermophilid grade of dental development as this term is applied to some Recent and fossil ground squirrels.

The teeth of *Citellus dotti* suggest a relationship to the more generalized Recent subgenera of *Citellus*. For a key to the subgenera of Recent ground squirrels see Howell (1938: 56). Considerable variation occurs in the skull proportions of the subgenera.

Ratio diagrams (after Simpson, 1941) were employed to evaluate the proportions of skulls and jaws of various Recent species of ground squirrels as well as of *Cynomys ludovicianus* (Ord) and *Marmota monax* Linnaeus. The ground squirrels were *Citellus (Notocitellus) annulatus, C. (Otospermophilus) beecheyi, C. (O.) variegatus, C. (Callospermophilus) lateralis,* and *Ammospermophilus leucurus. C. dotti* resembles *Marmota* more closely in skull and jaw proportions than any other species diagrammed. The only significant difference between these two species in skull and jaw proportions is the marked constriction of the postorbital region of the skull in *Marmota* (Fig. 6, B). *C. dotti* resembles to a lesser degree *Otospermophilus* and *Notocitellus.* The rostral proportions of these two subgenera, however, are different from those of *C. dotti.* In these Recent subgenera the rostrum is relatively longer and more slender than in *C. dotti* (Fig. 4, A and B). It is in these rostral dimensions that *Marmota* is least like *Otospermophilus* and *Noto-*

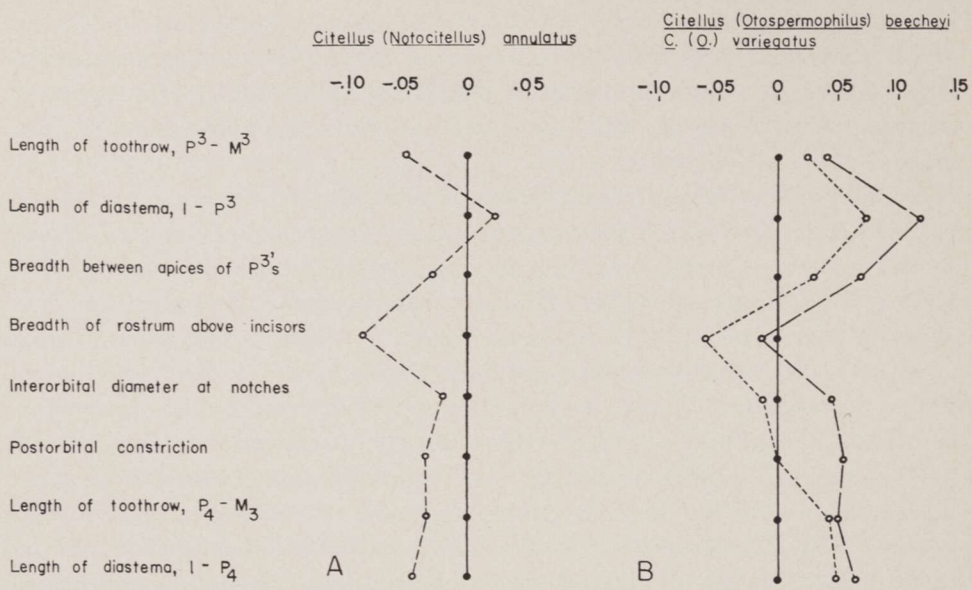

Fig. 4—Ratio diagrams, after Simpson (1941), comparing corresponding measurements of skulls and jaws of Recent ground squirrels to *Citellus (Buiscitellus) dotti*, solid line. A, *C. (Notocitellus) annulatus*, one specimen, dashed line; B, *C. (Otospermophilus) beecheyi*, mean for 50 specimens, dashed line; *C. (O.) variegatus*, mean for 24 specimens, dashed line. The proportions of corresponding regions of the skull and jaws between these several species is similar with the exception of longer upper diastema and narrower rostra in the Recent species.

citellus and more like *C. dotti*. *C. dotti* differs from *Callospermophilus* even more since this group tends to have reduced toothrow length in relation to the remainder of the skull and jaws (Fig. 5, A). *C. dotti* differs markedly from *Ammospermophilus* and *Cynomys* (Fig. 5, B; Fig. 6, A). In *Ammospermophilus* the P^3 is extremely small, thus reducing the length of P^3-M^3, the rostrum is moderately long and tapering, and the supraorbital diameter is greater. In *Cynomys*, toothrows are moderately long, the diastema is short, and the postorbital diameter is reduced.

Citellus dotti thus represents a species of ground squirrel which does not belong within any of the Recent subgenera of *Citellus*. Nor does it belong to the Hemphillian subgenus *Pliocitellus* Hibbard erected to receive *C. fricki* (Hibbard, 1942: 253). The new subgenus *Buiscitellus* is proposed to accommodate this Pliocene species. No descendants, either fossil or Recent, are known. Certain other Pliocene species known only by teeth, and hence placed within *Citellus (Otospermophilus)*, may eventually prove to belong elsewhere when the skulls and skeletons are found. *C. matachicensis* is not sufficiently closely related to *C. (Buiscitellus) dotti* to be included in the same subgenus. Nor does it seem to belong with any of the existing divisions of Recent ground squirrels.

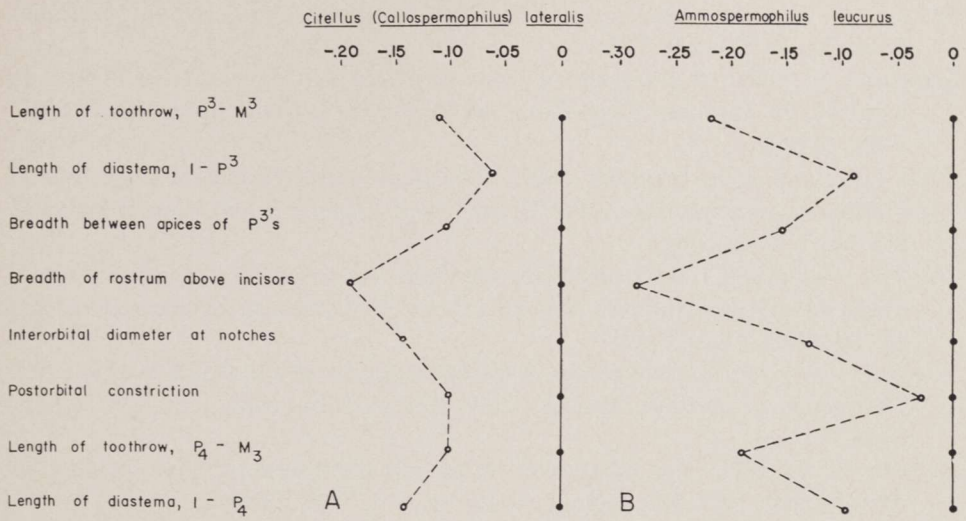

Fig. 5—Ratio diagrams, after Simpson (1941) comparing measurements of skulls and jaws of Recent ground squirrels to *Citellus (Buiscitellus) dotti*, solid line. A, C. *(Callospermophilus) lateralis*, mean for 2 specimens, dashed line; B, *Ammospermophilus leucurus*, mean for 17 individuals, dashed line. The relative proportions of the skull of C. *lateralis*, again, shows longer upper diastema and narrower rostra than C. *dotti*. The relative proportion of the skull and jaws of *Ammospermophilus leucurus* are markedly different than those of the fossil.

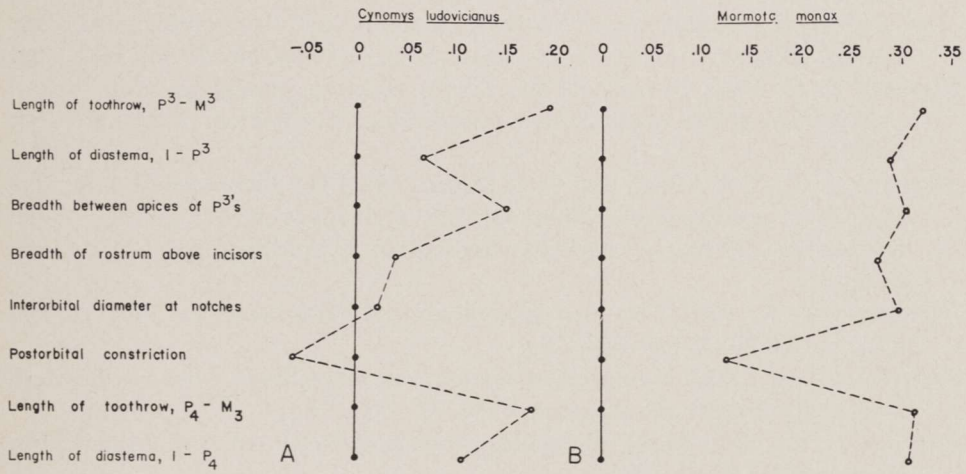

Fig. 6—Ratio diagrams, after Simpson (1941) comparing measurements of skulls and jaws of Recent sciurids to *Citellus (Buiscitellus) dotti*. A, *Cynomys ludovicianus*, mean for 8 individuals, dashed line; B, *Marmota monax*, mean for 2 specimens, dashed line. The relative cranial proportions of C. *dotti* are unlike those in *Cynomys*. Such proportions, however, are almost identical to those of *Marmota* with the exception of the postorbital constriction. This similarity included length of upper diastema as well as rostral breadth.

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